

Distributional ecology and behaviour of the early life stages of the box-jellyfish *Chironex fleckeri*

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Abstract

Laboratory observations on reared life stages of *Chironex fleckeri* (Cubozoa: Chirodropidae) have been combined with field sampling and observations to outline the life cycle of the species and the spatial and temporal distribution of populations in Queensland, Australia. A seasonal alternation of polypoid and medusoid generations from winter to summer respectively is accompanied by a shift in preferred habitat from tidal estuaries to the open eulittoral zone. The system appears to be constrained by predictable fluctuations in the suitability of the alternate habitats to their resident generations. Observations on behaviour, feeding, physiological tolerances, and sexual and asexual reproduction provide insights into the adaptiveness of this pattern.

Introduction

Chironex fleckeri Southcott, the Australian box-jellyfish or sea wasp, is a large (up to at least 22 cm diam.), active chirodropid cubomedusan found in nearshore waters of northern Australia and adjacent areas of the tropical Indo-Pacific (Cleland & Southcott, 1965). As in a number of related cubozoan species, *Chironex*'s adaptations to feeding on large active prey (primarily sergestid prawns and fish) in shallow sheltered water have resulted in frequent contacts between human swimmers and its uniquely potent envenomation mechanism (Hartwick, 1987). Hundreds of serious stings, some fatal, occur annually. A pronounced seasonality in the occurrence of these stings was noted by Barnes (1960) and Cleland & Southcott (1965), and the generally sporadic and

unpredictable abundance of the species within the danger season (approximately November to May for Queensland waters) inspired a practical interest in its spatial and temporal distribution. A generally observed predominance of small individuals in the early season (southern spring), progressing to larger, sexually mature adults in the late summer and fall, implicated an annual reproductive cycle in this pattern. Confirmation, *via* laboratory rearing, that *Chironex* possesses an alternate sessile polyp stage (Yamaguchi & Hartwick, 1980) suggested a seasonal alternation of generations, and provided the descriptions of the early life stages essential to a study of their distribution. Laboratory observations of the behaviour and environmental tolerances of these stages were conducted in a search for clues to their habitat preferences.

Laboratory studies of reared early life stages

Methods

The techniques of *in vitro* fertilization and larval rearing have been described (Yamaguchi & Hartwick, 1980). Observations reported here are of culture specimens from the original rearing and from a repetition in April 1985. In an attempt to encourage settlement behaviour, groups (usually 60–90) of developing larvae were exposed to a variety of environmental conditions and substrates in culture dishes. Three temperature ranges were used initially ($22.8^{\circ} \pm 0.3^{\circ}$, $25.3^{\circ} \pm 0.5^{\circ}$, $27.5^{\circ} \pm 0.5^{\circ}$ °C), which largely encompass that in local nearshore waters during the cooler months of inferred larval and polyp development. Most cultures were maintained in a natural (12:12) light:dark cycle, though some were kept in constant dim red illumination. Substrates offered for settlement were both artificial (glass, plastic, ceramic tile) and natural (rocks, shells of clams, oysters and barnacles, pieces of living or dead mangrove root) and were variously 'seasoned', from 'clean' through bacterial and algal films to entirely 'natural', encrusted with a diverse community of living organisms (bryozoans, sponges, serpulid polychaetes, hydroids, etc.). The condition and behaviour of developmental stages were observed with a dissecting microscope.

Experiments on salinity tolerances were conducted to determine the likelihood of an inshore habitat for the early stages. Small groups of planulae (20–25), creeping or sessile polyps (5–8) were admitted to 100 ml glass beakers and exposed to various distilled water dilutions of stock filtered coastal seawater (36.2‰) according to one of 3 temporal schemes judged to sample the likely range of inshore salinity fluctuations. In 'shock dilution' experiments, specimens were transferred immediately from stock seawater to a particular dilution. In 'rapid dilution' the culture water was diluted in steps of 15% per day by decanting half of the liquid and replacing it incrementally over several minutes with seawater of 30% greater dilution. 'Slow dilution' used the

same technique, but in steps of 5% salinity reduction per day. All experimental treatments were triple replicated. The condition of the experimental organisms and controls was assessed at regular intervals according to discernable criteria reflecting viability. Planulae were assessed primarily in terms of their locomotion, which was graded as: normal, slow, slowly rotating, or nil. Polyps were assessed according to the degree of extension of the body and tentacles (fully extended being 'normal') and their ability to respond by bodily contraction when stimulated by a touch with a fine needle or by a sudden increase in illumination. Highly contracted polyps with no responses to stimulation were deemed 'encysted' (Werner, 1975), while non-responsive specimens with roughened epithelium and/or fragmenting body were taken to be dead.

Results

Apart from expected differences in development rate, the early ontogeny of *Chironex* proceeded similarly in the 3 temperature ranges used. Development times for the intermediate range ($25.3^{\circ} \pm 0.5^{\circ}$ °C), which most closely approximates coastal temperatures during the inferred spawning season (fall), are therefore quoted below and this temperature was adopted for the salinity tolerance experiments.

The early life stages of *Chironex* showed a number of adaptations which might be expected to restrict dispersal away from the spawning area. Zygotes and blastulae were negatively buoyant and had a sticky outer coating which caused them to adhere firmly to hard substrates. The planulae, which emerged in 12–24 h, initially swam away from the substrate, but within hours had returned to within a few millimetres of it, where they continued to swim about for up to 24 h. This response may be explained, at least in part, as a reversal of a phototactic response, evident in the culture conditions. During their motile period, planulae developed the ability to attach temporarily to hard substrates by means of small (5 µm diam.) agglutinant nematocysts, which may give them

purchase to evaluate environmental conditions (e.g., current strength or substrate type) at a prospective settlement site. It would further serve to restrict displacement from the spawning area.

Following permanent attachment to the substrate, planulae metamorphosed into primary creeping polyps ('creepers') over 3–4 d and then commenced a motile benthic lifestyle which lasted for more than 2 weeks in culture conditions, though this may not be typical in nature. Inappropriate conditions for settlement (see below) could prolong the motile phase to an unnatural degree. Primary polyps developed at least 2 sizes of nematocysts in the body wall, though none was seen in the tentacles (nor is there any evidence of feeding in this stage). The smaller type appears to have the same agglutinant function (and may be identical) to those providing attachment for the planula. The function of the larger type is not certain, although these may be the stenoteles which later arm the tentacles of the sessile polyp. They may already serve to protect the organism from predation, since contact of a swimming *Artemia* nauplius with a creeping polyp resulted on several occasions in the rapid death of the nauplius.

Under the conditions of the experiments, larval settlement showed no clear substrate preferences. Planulae did not exhibit attraction toward the natural substrates, and were as likely to metamorphose on the floor of the container. Primary polyps, when pipetted onto natural substrates, crawled about slowly (up to 0.5 mm h^{-1}) over the surface for a number of days, but few settled permanently as a sessile feeding polyp. Whether the substrates or the attendant environmental conditions were inappropriate cannot be determined. Similar barriers to achieving final polyp settlement have been experienced with related cubozoan species in culture (Okada, 1927; Studebaker, 1972; Yamaguchi, pers. comm.).

The few primary polyps which succeeded in establishing themselves as sessile feeding polyps were easily maintained in culture, fed readily on *Artemia* nauplii, and proliferated by asexual budding of secondary creeping polyps. The latter developed from the lower body wall of well fed,

sessile polyps over 2–7 d, detached, and crawled away at up to 22 mm h^{-1} . The motile period lasted hours to days in culture conditions and resulted in average dispersal distances of tens of millimeters. Secondary creepers showed little reluctance to attach permanently to a diversity of natural and artificial hard substrates. There was a clear bias, however, toward settlement on vertical surfaces or in indentations and corners, suggesting a form of rugophilia. There was no evidence for gregarious settlement, although recruits occasionally attached within less than a tentacle span from some prior resident.

The planulae and polyps of *Chironex* were tolerant of reduced salinity to a degree suggestive of an inshore/estuarine habitat. Planulae showed normal swimming patterns after shock dilution down to salinities of 20‰, when some initial disruption appeared. This was intensified below 20‰, although planulae were able to adapt and return to normal swimming: below 13‰ recovery was no longer possible. Gradual dilution in 5‰ increments every 2 h permitted normal swimming to at least 15‰, but there is no suggestion that normal activity can be extended much below the 13‰ threshold revealed by shock dilution.

Secondary creeping and sessile polyps followed comparable patterns. Shock dilutions to 21‰ had little effect on normal attachment of creepers and development of armed tentacles. Eventually these cultures were capable of normal feeding and asexual reproduction. Below this level of dilution normal extension of body and tentacles was not achieved, even for cultures observed after 6 weeks, although most specimens survived. At the 13‰ threshold creepers attached but soon became highly contracted and non-responsive, a condition probably equivalent to encystment (*sensu* Werner, 1975). In this state, specimens would survive for at least 2 weeks and would re-emerge and feed if salinity levels were restored to normal. Below 11‰ all specimens rapidly showed signs of death and decomposition. Gradual dilution experiments with sessile polyps revealed similar thresholds of distortion and encystment, but some encysted stages were able to survive and recover from several days of exposure to 5‰ water after salinity was again raised.

Field sampling of early life stages

Methods

Efforts to locate the early life stages of *C. fleckeri* in nature focused initially on the free-swimming juvenile medusae, it being judged technically easier to sample macrozooplankton in the water column, than sessile polyps on unknown benthic substrates. It was hoped that size-frequency gradients would then lead to the locations of the benthic polyps. Because a popular prevailing hypothesis suggested a remote offshore breeding site for the species, with shoreward advection of juveniles linked to seasonal winds, the initial focus of the sampling was the open water over the inner half of the continental shelf. Allowing for an alternate inshore source of recruits, however, sampling transects were positioned to originate near different sandy, rocky, and estuarine coastal habitats.

During offshore sampling (1978-1980), ca 1200 plankton samples were taken during 47 cruises, primarily by means of a subsurface Tucker trawl and a Manta net neuston sampler. This year-round, intensive effort (a total settled volume of plankton of > 1000 l filtered from $> 4 \times 10^9$ l of seawater) yielded < 90 cubozoan specimens, of which only 8 were *C. fleckeri*, all relatively mature juveniles (4.4-73.0 mm diam.), the smallest caught closest to shore. Such results, together with the physiological and behavioural adaptations noted above, led to a rejection of the offshore breeding hypothesis and to a shift in the sampling focus toward estuarine waters.

Plankton sampling of coastal estuaries spanned 1978-1983. Three types of towed nets suitable for use from small boats were constructed, with 0.33 mm mesh, to sample surface, midwater and epidermal zooplankton. A total of 84 excursions yielded > 700 samples (mean filtered volume = 146 m^3). Although samples were taken in 24 Queensland rivers and creeks, from the Norman River at Karumba to Coorooman Creek near Yeppoon, regular year-round sampling was concentrated at Alligator Creek, a tidal mangrove estuary near Townsville.

The search for the polyp stages, presumed to be on hard substrates in the vicinity of the captured young medusae, began in 1980; over the next 7 y, collections were made in 14 estuaries in North Queensland. Many thousands of hard substrates (rocks, barnacles, molluscs and their shells, mangrove roots, leaves, branches, etc.) were collected by divers or with a small towed dredge, stored in seawater, and returned to the laboratory for inspection with dissecting microscopes. Most adhering fauna and flora appeared alive at the time of inspection.

Results

Since the first appearances in late 1978, 106 young (0.6-1.8 mm diam.) *Chironex* medusae were captured in 4 different river systems. Most captures occurred during October and November (all between September and January), 6-15 km upriver from the sea. Thus a convincing picture of medusae production in rivers emerged, characterized by restricted area and a marked and predictable seasonality. Abundances in the principal sampling areas were < 3 medusae per 100 m^3 of water. Environmental conditions at the onset of medusa production can be defined in terms of physical parameters (water temperatures climbing above 25°C , salinity values at an annual peak exceeding 40‰) and planktonic food supplies (peak abundances of such probable medusa prey as fish and decapod larvae).

In mid-1985 a population of polyps was found on stones collected from a small creek where young medusae occurred 26 km from Townsville. During later 1985 examination of 529 stones, 54 *Rhizophora* sp. prop roots and branches, and 20 bivalve molluscs (*Isognomon* and *Saccostrea* spp.) from subtidal and intertidal areas helped define the distributional parameters of the polyp population, which was centred ca 1 km from the sea in shallow subtidal water. The creek bottom here was paved with closely-packed, worn granitic cobbles from a few centimetres up to 0.5 m diam. The stones were covered on the upper sides by a dense algal mat and, because of their close pack-

ing and mutual support, many were undermined by currents, leaving a narrow space between the underside and the sediment. These surfaces, free of alga, were populated by sessile suspension/plankton-feeding animals: bryozoans, sponges, hydroids and serpulid worms, plus a number of errant species. This assemblage resembled that on rocks used in the settlement experiments described above.

A total of 464 *Chironex* polyps were found, mostly on stone undersurfaces; a few appeared on the shells of living bivalves, but nearby mangrove structures carried none. Within the preferred habitat the medium-scale ('interstone') distribution was patchy, with 23% of haphazardly selected stones carrying polyps, generally in small groups (mean size = 5.15 individuals, s.d. = 5.07, maximum = 23, N = 86). Variance: mean ratios usually exceeded 3.0 for samples of 10–30 stones.

Although differential settlement or mortality cannot be ruled out as the cause for this pattern, it appears more likely that individual planulae settled randomly on stones, and produced other group members by asexual cloning of new polyps. The presence of the characteristic encrusting community on most unoccupied stones suggests that they offer suitable microhabitats for polyps.

Small-scale ('inrastone') distribution of group members also appeared non-random and dominated by rugophilia. Most polyps were attached in concavities or along abrupt deflections of the substrate. The calcareous tubes of serpulid polychaetes (*Ficopomatus* and *Hydroides* spp.) frequently had polyps attached along their bases. A few polyps were found in relatively open flat areas covered only by a bacterial film, but none occurred on living encrusting organisms such as sponges, bryozoans, or colonial ascidians.

Despite such restrictions on settlement, it is unlikely that polyp densities were often limited by settlement site availability. The mean polyp density on occupied stones of *ca* one per 10 cm² of undersurface, while probably overestimating available space, was the likely result of food-limited proliferation rates and natural mortality. When 4 stones (mean undersurface area

= 61 cm²) with 7–10 polyps each, from which most errant species were removed, were maintained in aquaria with daily feeding on *Artemia* nauplii, the incidence of budding increased significantly over levels observed in nature and polyp densities increased severalfold within 10 d.

In order to evaluate potential food supplies for the polyp bed, a variety of plankton samplers were used in the creek, including a plankton pump and anchored net system designed to sample within a centimetre of the rock substrate. Sample analysis indicated a predominance of small cyclopoid and harpacticoid copepods. On 4 occasions polyps under observation in the laboratory stung and ingested such copepods. We found that in nature most distended polyps contained these epidermal prey or other small errant crustacea.

The population density did not change markedly through the year until late in January 1986, even though metamorphosis into medusa stages had begun in September. In January, the first substantial rain runoff of the summer sharply reduced salinities (0–5‰) throughout the polyp beds, below their survival tolerances. Subsequent samples revealed no remaining polyps, suggesting mass mortality of the population. There was no reoccurrence of this polyp population through 1988.

Monitoring studies of polyps on artificial substrates

Methods

We attempted to monitor rates of mortality and asexual reproduction by returning marked rocks to the natural environment and to reinspect them periodically thereafter. Serious practical difficulties arose, in that rocks could not be reliably repositioned on the creek bottom such that the required free space above the sediment was preserved. Massive mortality resulted, as also occurred when rocks were placed in an inverted position, with the polyps exposed to siltation and other hazards of the open creek environment.

An alternative technique was developed to permit accurate repositioning of polyps in the stream environment in such a way as to closely mimic the normal microhabitat. Creeping polyps produced in the laboratory by budding from field collected specimens were allowed to attach to small (33 cm²) ceramic tiles. A series of 9 parallel grooves (1.3 mm wide × 1.4 mm deep) cut across the tile surface permitted accurate plotting of the position of each polyp (about 20 per tile) and, thereby, its subsequent identification. Each tile was clamped into the surface depression between pairs of standard masonry bricks, suspending the polyps within the enclosed space. Narrow openings at each end permitted a flow of water and suspended food past the polyps, but excluded most sunlight, sediment and large predators. One inoculated tile was positioned alongside an identical clean tile in each 'brick sandwich', the blank being used to monitor 'long-distance' dispersal of polyps. Such assemblies were prepared in replicate and positioned at sites on the creek bed in and adjacent to the nursery area. Tiles were retrieved and examined with dissecting microscopes at intervals of 2 to 4 weeks. Maps of each tile surface were used to record polyp turnover. The incidence of vegetative buds and metamorphosis, estimates of age based on size and tentacle number, and any evidence for feeding or predation were noted. Macrophotographs monitored the distribution of encrusting species, which might be major space competitors.

The monitoring experiment was conducted on a limited scale in late 1985 and repeated at full scale during each of the following 3 y. In 1988 substrates were located in 3 different creeks to further expand the scale of spatial comparison.

Results

Preliminary analysis of nearly 10000 polyp records offers an insight into polyp distributional ecology as well as an outline of temporal patterns of mortality and recruitment.

Asexual reproduction occurred continuously throughout winter, spring and early summer,

recruitment averaging 4.2% d⁻¹. Recruitment would provide a low estimate of asexual proliferation given the probability of some creeper emigration, confirmed by invasion of the adjacent blank tile. A precise estimate of budding rate was not feasible since the monitoring interval was probably longer than bud generation time (see above).

The disappearance of polyps was also a continuous process and can be interpreted as natural mortality during the winter, though spring-summer losses would represent a combination of mortality and metamorphosis to the medusa stage. It is unlikely that polyp migration contributed significantly to the observed turnover. Polyps found at new locations were generally smaller and had fewer tentacles than established polyps. Among causes of mortality, overgrowth by encrusting organisms occurred with some regularity: bryozoans, sponges, serpulid polychaetes, colonial ascidians and tubiculous amphipods all could outcompete *Chironex* for space. Predation by errant species is also probable (although this has not been observed) since the locations of many vanished individuals were not found occupied by space competitors.

The rugophilic bias in polyp settlement was clearly confirmed as the result of active choice by the secondary creeper rather than of differential survival. Although the area of the 9 parallel grooves comprised only about 45% of the total surface area of the tile face, 86% of new polyp recruits were found within them. Of the few found on the intervening flat areas, 34% occurred along the bases of serpulid tubes, which soon recruited onto the tiles (together with many other representatives of the associated community). The observed rate of asexual budding would not permit such a bias to arise from differential survival of many more recruits, nor would the average longevity observed in the few polyps which appeared on flat surfaces. Under the conditions of the experiment, exposed polyps did not survive for significantly briefer periods than did polyps in the grooves.

Small-scale distribution patterns paralleled those on natural substrates, in that recruits were found dispersed from possible parent polyps by

significant but limited distances. Blank tiles were slowly but steadily invaded by creepers from the adjacent tile, at a rate indicating maximum dispersals measured in a few tens of millimeters.

As in the case of the natural population in 1985, the tile populations over 4 annual experiments successfully maintained (or sometimes increased) their densities despite continuous mortality and spring metamorphosis until heavy summer rains reduced salinities to lethal levels. The impact of runoff clearly varied between estuaries and between sites at different distances upriver in accordance with local dilution, but polyps rarely survived into February, even in years of lower than normal rainfall. It is therefore likely that polyp populations are normally annual, surviving through a number of turnover cycles during the drier months of the year, and are later reestablished by the spawning medusae when salinities in the estuaries return to tolerable levels.

Discussion

C. fleckeri is a neritic tropical species which has adapted its life cycle to a seasonal cycle in the environment, such that an annual alternation of generations conforms with an alternation of optimal habitats. The polyp stage is a small, sessile, ambush-entangling predator which expends relatively little energy in feeding, can endure weeks of starvation in a food-poor environment, but can take immediate advantage of local increases in food supply by asexual proliferation. Its minimal requirements include a stable hard substrate for attachment and a microhabitat which is sufficiently protected against smothering by sediment and turbulence strong enough to dislodge it, to allow it to maintain its population until the environment favours the survival of the medusa. As a marine organism with little external barrier to osmotic exchange, the polyp and its preceding larval stages show a significant though limited tolerance of reduced salinity, characteristic of estuarine invertebrates. It can feed and reproduce at intermediate dilutions ($> 20\text{‰}$) and survive periods of exposure to much lower salinities

($> 5\text{‰}$). Hypersaline tolerances have not been systematically determined, but normal behaviour to at least 42‰ has been observed in aquarium cultures.

The *Chironex* medusa is a large, nektonic cruising-entangling predator which would expend relatively large quantities of energy in feeding and would consequently be dependent on adequate concentrations of its micronektonic prey. Its sexual reproduction, while never observed in nature, most probably involves semelparous spawning of a large number of gametes following an energy-costly migration to the polyp habitat, necessarily delayed until salinity conditions in that habitat permit survival of the subsequent larvae and polyps. The medusa's minimal requirements include prey concentrations in an environment which is sufficiently open to allow deployment of its numerous, long (up to at least 3 m when extended) tentacles while swimming, and free of turbulence, strong currents and obstructions which would tangle and damage them.

The coastal environment of tropical Queensland, while enjoying many stable (relative to higher latitudes) parameters, nevertheless undergoes predictable seasonal oscillations in a number of factors relevant to the survival of *C. fleckeri*. Of particular significance are rainfall runoff and wind energy. Summer is characterized by high monsoonal rainfall and generally light breezes, while winter offers negligible runoff (salinities are generally higher than the adjacent open sea) and persistent strong southeasterly trade winds (Pickard, 1977). Runoff dilution most affects estuaries, with salinities routinely near zero during summer monsoons, while winter winds increase wave turbulence along the exposed coastline. Apart from these alternating seasonal disruptions, the estuaries and exposed coastline offer optimal conditions to the polyps and medusae, respectively, yet appear far less suitable for the alternate life stage.

The strong two-directional tidal flow in the estuaries serves to scour and undermine stones and other heavy solid substrates, yet boundary layer effects would limit flow through the created microhabitats to levels unlikely to dislodge the

polyps or impede their activities. Creeping polyps and their prior larval forms show adaptations which would enhance the likelihood of settlement in such areas. Given the limited mobility of the primary polyp, it is probable that the planulae first locate rock undersurfaces by negative phototaxis and attach to them by means of their agglutinant nematocysts. Dispersal of creeping polyps is probably limited to immediately adjacent surfaces, but the tendency to move upward into rugose locations no doubt enhances security from sedimentation, predation and dislodgement. Large medusae, on the other hand, would be ill-adapted to life in tidal estuaries, since swift currents and abundant mangrove roots and other submerged snags would greatly hamper use of their tentacles for feeding.

The exposed coastline, due to the shelter provided by the Great Barrier Reef, is a low energy environment characterized by fine sediments and gently sloping beaches. Calm summer conditions, onshore breezes and enhanced productivity due to nutrient runoff favour the aggregation of juvenile fish and sergestid shrimp (*Acetes australis*) very close to shore. This affords favourable feeding conditions for *Chironex* medusae, which swim steadily alongshore in shallow (< 2 m deep) water. Conditions for the polyps appear far less suitable, since hard substrates are scattered, unstable, and tend not to be undermined by the gentle, multidirectional water flow.

A coherent picture thus emerges of the life cycle of *C. fleckeri*, featuring a seasonal alternation of generations and habitats concordant with oscillations in their respective compatibility. Many details remain to be clarified in this outline of the distributional ecology of the species, and caution is appropriate when generalizing these patterns to other populations which may be subject to different environmental constraints. Even for tropical Queensland, much uncertainty remains regarding typical population parameters and key controlling factors. *Chironex* has proven to be extraordinarily rare, sporadic and difficult to sample in its various life stages. In 9 y of searching, only one annual population of polyps was found; this suggests that it was not typical in its density and/or extent. The possibility of alternate

microhabitats has not been excluded. Although more predictable in their presence, early medusae were never common enough to permit resolution of the smaller scale features of their distribution and migration to the adult habitat. The elusive adults still conceal many aspects of their complex migratory behaviour, including the inferred return to the polyp nurseries to spawn. As the only stage with significant motility, the medusae would seem to bear responsibility for migration along the pathways of this complex life cycle.

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